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PRELIMINARY REPORT ON THE LIFE HISTORY OF THE COMMON SHRIMP *PENAEUS SETIFERUS* (LINN.)

By F. W. WEYMOUTH, MILTON J. LINDNER
and W. W. ANDERSON

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PRELIMINARY REPORT ON THE LIFE HISTORY OF THE COMMON SHRIMP *PENAEUS SETIFERUS* (LINN.)

By F. W. WEYMOUTH, PH.D., MILTON J. LINDNER, and W. W. ANDERSON, *United States Bureau of Fisheries*

CONTENTS

INTRODUCTION

The present report is concerned with the salient features of the life history of the common or so-called "lake shrimp" (*Penaeus setiferus*) of the South Atlantic and Gulf coasts and the bearing of these facts on the problems of the shrimp industry. The information has been obtained in the carrying out of a program of cooperative shrimp investigation in which the Bureau of Fisheries has been supported by the States of Louisiana, Georgia, and Texas. The loyalty and industry of the staff and of our associates have made possible the substantial results here recorded and the members deserve the particularized credit for which our space is too limited.[1]

Although the study is far from complete, it seems best to place the information obtained on record, in part because it is the most complete life history available for any species of shrimp and in part to give the purposes and needs of the investigational program.

A brief statement will first be given of the extent and importance of the shrimp fishery in the United States, and next the state of knowledge at the beginning of the present work; then the life history of *Penaeus setiferus* will be outlined very briefly, after which the evidence from which these facts were drawn will be given in such detail as is now possible (this will constitute the great bulk of the paper); and finally, the bearing of this information upon the problems of depletion and protection will be discussed briefly.

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[1] The staff of the shrimp investigations includes F. W. Weymouth, Milton J. Lindner, and Gordon Gunter with headquarters in New Orleans, La., W. W. Anderson at Brunswick, Ga., J. S. Gutsell at Beaufort, N.C., and Kenneth H. Mosher at Aransas Pass, Tex. J. N. Gowanloch and Forrest Durand, of the Bureau of Research and Statistics of the Louisiana Department of Conservation, have been so closely associated in the cooperative program as scarcely to be differentiated from the staff members. We gladly acknowledge the aid of Dr. Waldo Schmitt, U.S. National Museum, in the identification of material; and of Dr. R. Von Ihering, of the Instituto Biologico, for information concerning the shrimp fishery of Sao Paulo, Brazil. We are also greatly indebted to many men in the shrimp industry, in particular to the late John Dymond, Jr., former president of the Southern Canners Exchange; R. R. Rice, of Aransas Pass, Tex., and Senator Jules Fisher, of New Orleans, La., who have aided in the collection of data and have placed at our disposal their records for statistical analysis. Approved for publication, Mar. 22, 1933.

PRODUCTION AND VALUE OF SHRIMP

The shrimp fishery of the United States produced a total of 113,263,000 pounds in 1929 and 92,327,000 pounds in 1930, ranking in each year ninth in volume among all the fisheries. The value to the fishermen of the shrimp taken in 1929 was $4,575,000; this placed the fishery fifth in value. It was exceeded only by the salmon, oyster, haddock, and halibut. In 1930, due to a decline in price and in catch, the value was $3,134,000, so that it fell to tenth rank.

As may be seen from table 1, more than 95 percent of the shrimp taken were from the South Atlantic and Gulf States, slightly over 40 percent coming from Louisiana alone. Here occur the following species: *Penaeus setiferus, Penaeus brasiliensis, Macrobrachium* sp., *Xiphopenaeus kroyeri, Trachypenaeus constrictus*

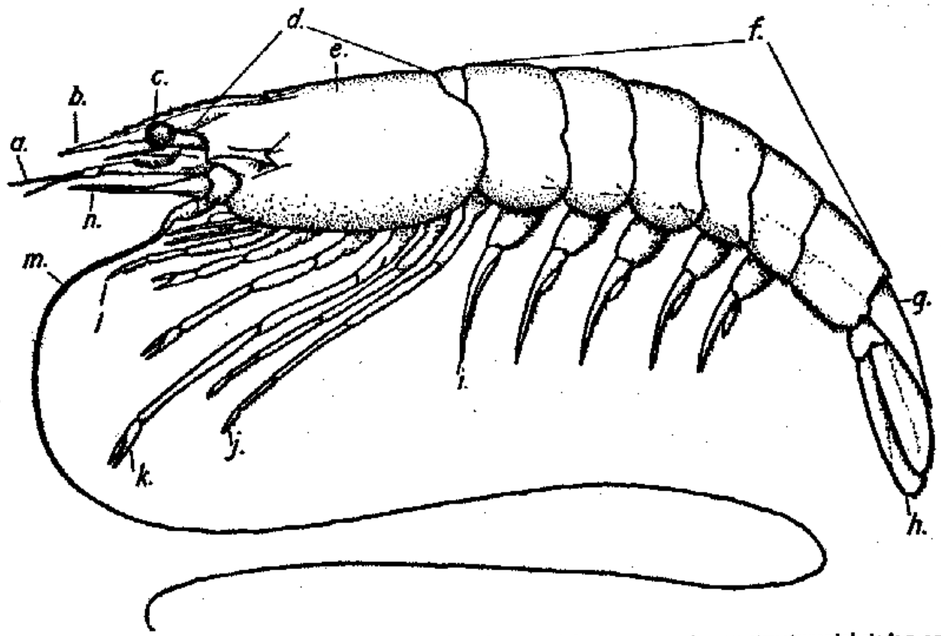

FIGURE 1.—Side view of the common shrimp (*Penaeus setiferus*) with some of the more conspicuous structures labeled; *a*, antennule; *b*, rostrum or "spine"; *c*, eye; *d*, cephalothorax or "head"; *e*, carapace or "head shell"; *f*, abdomen or "tail"; *g*, telson or "tail spine"; *h*, uropod or "tail fin"; *i*, first pleopod or "swimming leg"; *j*, fifth pereiopod or "walking leg"; *k*, chela or "pincer" of third periopod; *l*, third maxilliped; *m*, antenna or "whisker"; *n*, antennal scale or scicle.

and *Sicyonia* sp. They may be distinguished as follows: *Macrobrachium* is easily recognized from its presence in fresh or slightly brackish water. Only the first two pair of walking legs have pincers, the first being relatively very large. It supports a distinct river fishery of small volume not here considered. All of the other species belong to the *Penaeidae* and agree in having the first three pairs of walking legs, instead of only two, armed with pincers, a family character. These shrimp are characteristically salt-water forms, although they may be found in brackish bays at certain times of year. The two species of *Penaeus* may be told from *Trachypenaeus* and *Xiphopenaeus* by the fact that the rostrum is armed with spines both above and below. *P. setiferus* differs but little from *P. brasiliensis*. The most easily recognized distinguishing characteristic is to be found in the groove on either side of the rostrum. In *P. setiferus* these grooves, conspicuous along the side of the rostrum, become shallow as they reach the carapace and are soon lost. In *P. brasiliensis*, however, the grooves continue to the back margin of the carapace. (See figs. 3 and 4.)

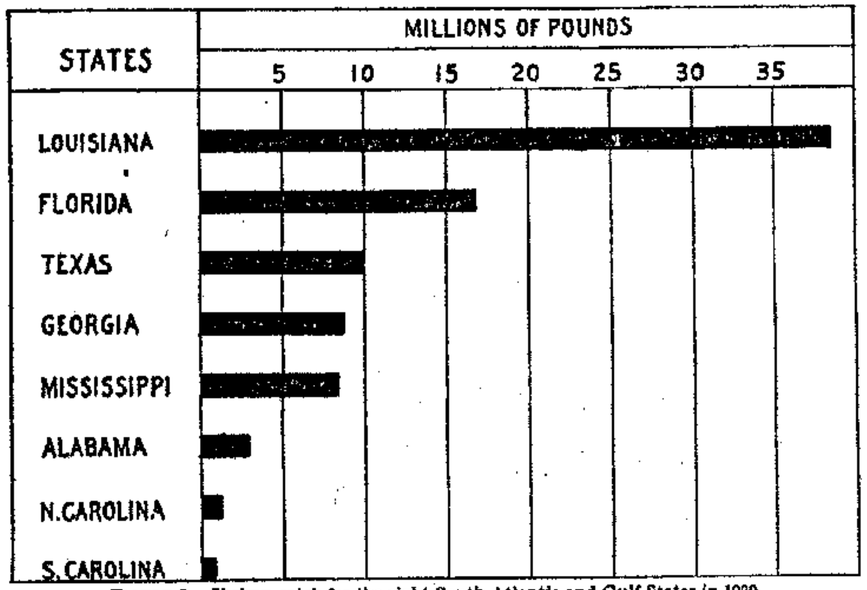

FIGURE 2.—Shrimp catch for the eight South Atlantic and Gulf States in 1930.

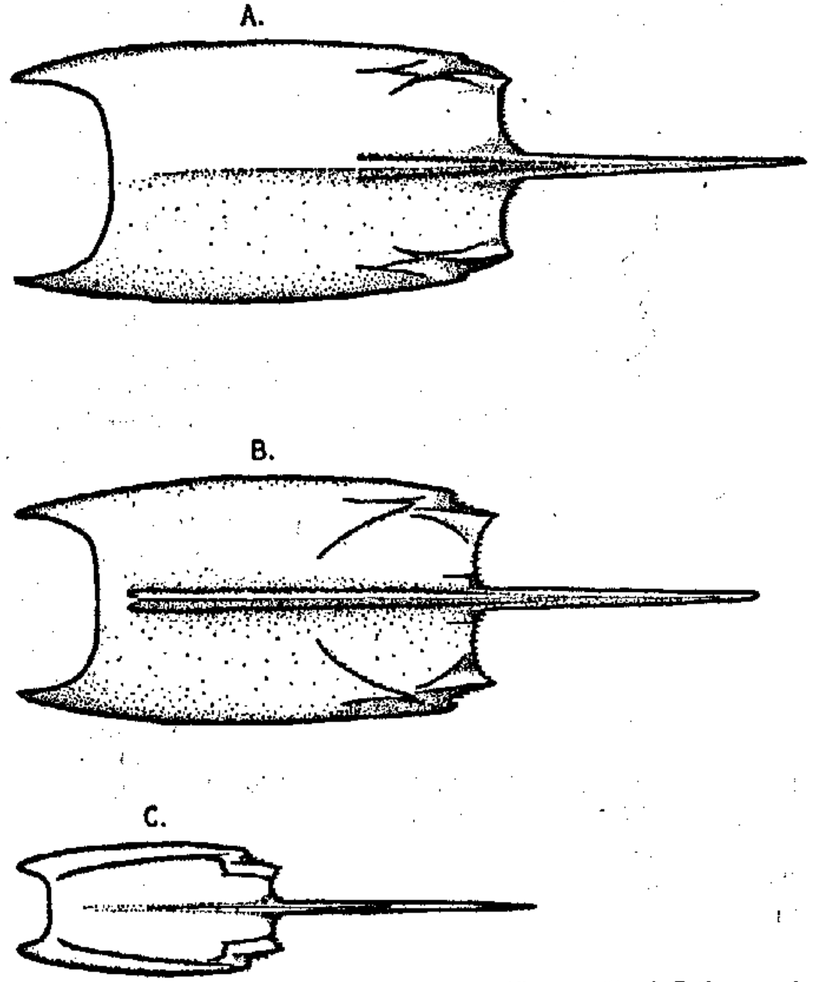

FIGURE 3.—Dorsal view of the carapaces of *A*, the common shrimp (*Penaeus setiferus*); *B*, the grooved shrimp (*P. brasiliensis*); and *C*, the sea bob (*Xiphopenaeus kroyeri*) showing the presence of rostral grooves in the grooved shrimp and their absence in the common shrimp and the sea bob.

TABLE 1.—*Shrimp taken in the United States in 1930 according to districts* [1]

Section	Catch		Value	
	Pounds	*Percent*	*Dollars*	*Percent*
South Atlantic and Gulf States	88,117,000	95.43	2,995,000	95.56
Pacific Coast States	2,785,000	3.02	49,000	1.56
Alaska	932,000	1.01	42,000	1.34
Middle Atlantic States	341,000	.37	29,000	.93
Mississippi River	147,000	.16	15,000	.48
New England States	5,000	.01	4,000	.13
Total	92,327,000	100.00	3,134,000	100.00

[1] No catch was reported in the Chesapeake Bay States or in the States bordering on the Great Lakes.

Trachypenaeus shows a family resemblance to *Penaeus* but is much smaller and the rostrum, although armed with 7 to 9 spines above, is smooth below. *Xiphopenaeus* differs from all the other penaeids in having a rostrum as long or longer than the carapace and the fourth and fifth pairs of walking legs much elongated and slender. These four long legs, together with the two antennae or "feelers" projecting beyond the "head" gave rise to the term "six barb" among the French fishermen. This has been corrupted to "sea bobs", and it is by this name that they are generally known. *Sicyonia* is an uncommon small form readily distinguished by the very short rostrum and the crest which continues from the rostrum down the middle of the body.

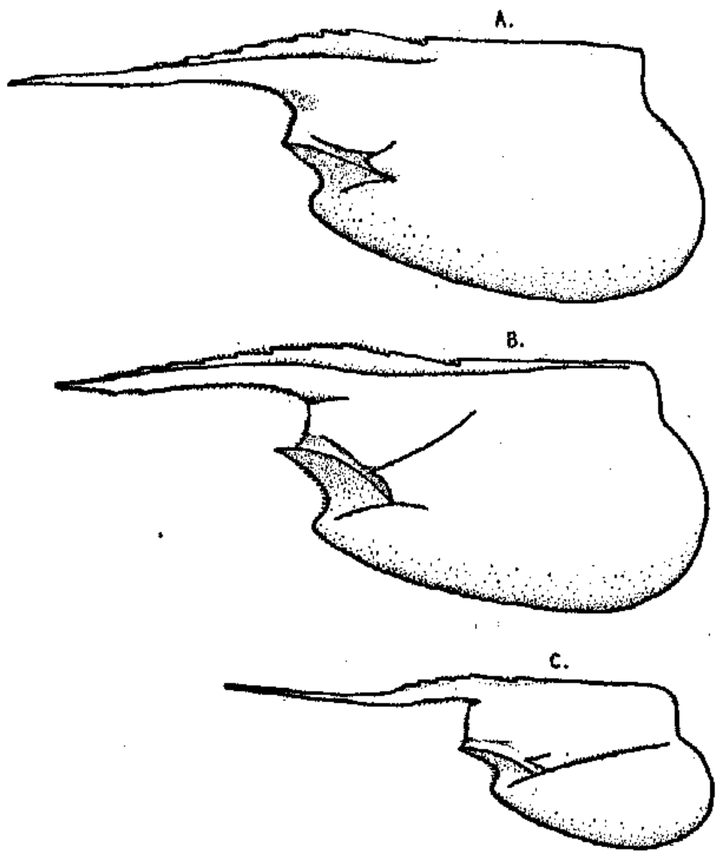

FIGURE 4.—Lateral view of the carapaces of *A*, the common shrimp; *B*, the grooved shrimp; and *C*, the sea bob. In both the common shrimp and the grooved shrimp teeth appear on both the upper and lower surfaces of the rostrum, while in the sea bob they are absent from the lower surface.

Of the penaeids, *Sicyonia* and *Trachypenaeus* are incidental only and of no economic importance. *Xiphopenaeus* may contribute 2 or 3 percent to the catch. It is too small to be used in canning but finds its way into the fresh markets and drying platforms. *P. brasiliensis* may at times be abundant but forms less than 5 percent of the total. The single species *Penaeus setiferus* accounted for about 90 percent of the total. The single species *Penaeus setiferus* accounted for about 90 percent of all the shrimp taken in the United States, or 100 of the 113 million pounds caught in 1929.

TABLE 2.—*Shrimp taken in the South Atlantic and Gulf States for 1929 and 1930, arranged by States*

	1929				1930			
	Catch		Value		Catch		Value	
	Pounds	*Percent*	*Dollars*	*Percent*	*Pounds*	*Percent*	*Dollars*	*Percent*
Louisiana	49,455,982	45.56	2,025,336	45.66	38,664,487	43.88	1,159,628	38.71
Florida	18,618,564	17.15	879,192	19.82	16,848,576	19.12	635,606	21.22
Mississippi	13,101,450	12.07	421,491	9.50	8,489,050	9.63	318,871	10.65
Georgia	12,377,619	11.40	581,015	13.10	8,852,712	10.05	334,578	11.17
Texas	9,415,317	8.67	327,008	7.37	10,189,318	11.56	377,016	12.59
Alabama	4,395,400	4.05	154,130	3.48	2,982,200	3.38	97,219	3.25
North Carolina	807,495	.83	30,560	.69	1,208,610	1.47	40,752	1.36
South Carolina	287,711	.27	16,625	.37	792,733	.90	31,814	1.06
Total	108,550,538	100.00	4,435,366	99.99	88,117,686	99.99	2,995,380	100.00

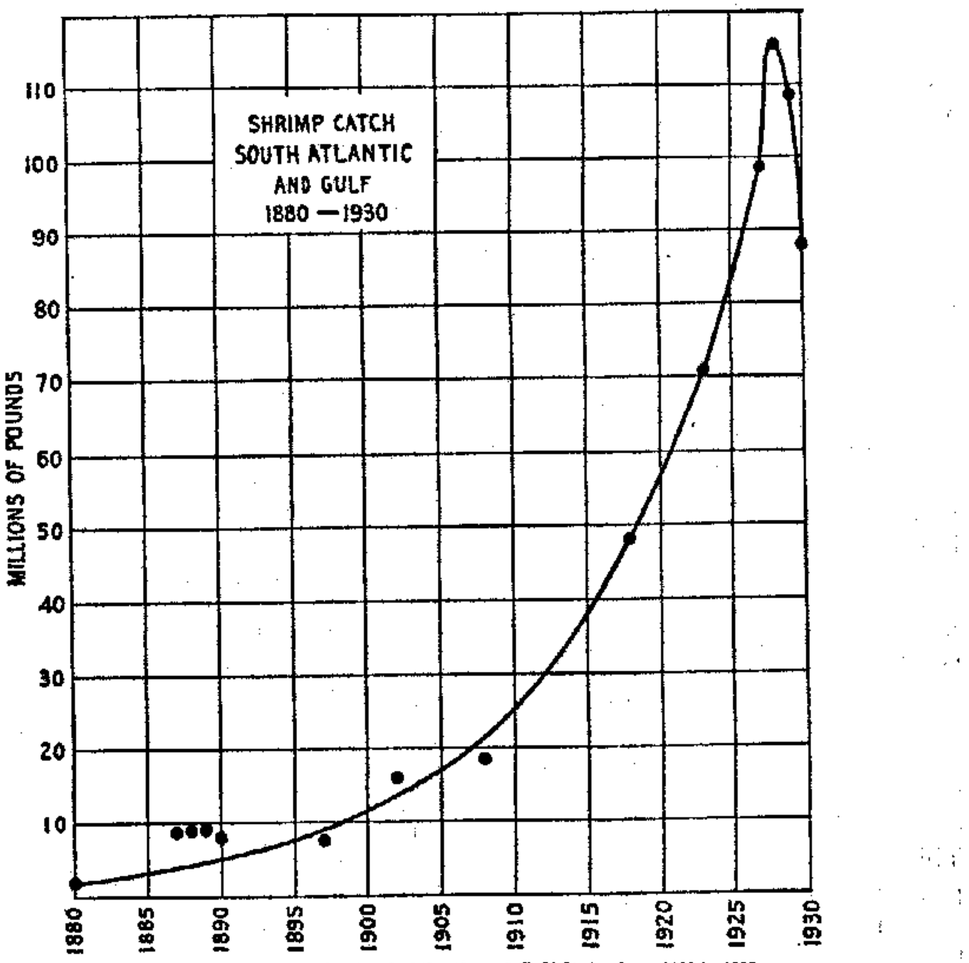

FIGURE 5.—Shrimp catch for the South Atlantic and Gulf States from 1880 to 1930.

Another phase deserves emphasis. While the shrimp ranks high among the fisheries of the United States, it is preeminent among those of the South Atlantic and Gulf States. Here among eight coastal States it ranks first in value, being followed by the oyster and the mullet; and second in volume, being exceeded only by the menhaden, which, however, ranks only fourth or fifth in value. In volume the shrimp is followed by the oyster and the mullet.

A fishery of this magnitude, the most important in the South, giving employment to thousands of fishermen and factory operatives, deserves careful attention if it is to be maintained in this valuable state. The rapid expansion of the fishery during the past 40 years, throughout which time it has doubled in volume every 8 or 9 years, has suggested caution, and recently the men in the industry have taken the initiative in asking for investigation, fearing, apparently, that some of the fluctuations in the catch were the forerunners of serious depletion. The prime requisites for successful handling of the problems of the shrimp, as of other fishery resources not adapted to cultivation, are information as to the abundance and knowledge of the life history. The first is needed to tell when protection is required and the second to guide such protection into intelligent and effective channels.

Unfortunately data for even the roughest analysis of abundance is lacking. State and Federal data give only the total catch and except for the last year or so no indication of the effort that produced the catch. Some private records alone serve to show the boat catches by which the effort could be analyzed, but these records are too scattered and cover too short a time to solve the problem. The outlook in this direction is, however, now more hopeful, for in Louisiana, a law, originally drafted with the assistance of members of our staff, in the future will give figures from which depletion may be detected as it appears. In consequence of these conditions we are unable to present in this report any data on the important question of abundance.

On the other hand, we must have an adequate knowledge of the life history and habits of the shrimp in order that, should depletion become apparent, intelligent protective measures may be applied at once. The only purpose of this preliminary report is to make available what information has been obtained against the time when it may be necessary to frame protective measures. Data on many points are far from conclusive but still may be useful for legislative action; the paper must be considered solely as such a progress report in spite of the fact that the data at hand establish a more complete life history than has hitherto been available for any shrimp of economic importance.

PREVIOUS WORK ON LIFE HISTORY

At the time the present investigation was started the information available concerning the American penaeids, and especially *Penaeus setiferus*, other than that in purely systematic papers was very meager. Fritz Müller in 1863 had reported from Brazil the occurrence of a nauplius larva presumably belonging to the genus *Penaeus*. In 1883 Brooks obtained penaeid larvae at Beaufort, N.C., and was able to trace the main stages of the larval history. He assumed them to be the young of *Penaeus brasiliensis*, but neither he nor Müller established the specific characters for the larvae. This work was solely morphological, interest being centered in the occurrence of the primitive nauplius larvae previously found only in lower crustacea.

In this connection it may be well to point out a peculiarity of the *Penaeidae* which has made study of the life history difficult. Unlike the majority of the higher Crustacea, the female penaeid does not carry the developing eggs attached to the abdominal legs. In consequence, although eggs of the other shrimp and crabs, as for example *Crago vulgaris* of the North Sea, may readily be obtained for study, no one has ever reported a fertilized egg of *Penaeus*. The mature ovarian egg is very small, measuring from one fourth to one third of a millimeter in diameter, and the unique larval history of *Penaeus* is related to this fact. The minute larvae hatching as nauplii pass through 6 or 8 distinct stages, in contrast to the condensed development of most decapods in which the eggs, well supplied with stored yolk, hatch into larvae corresponding to stages occurring late in the larval history of *Penaeus*.

No further work was done until more than 20 years later at the Gulf Biologic Station, Cameron, La. In 1908 Spaulding and Guilbeau and in 1910 Gates reported on the shrimp. Facilities were not available at the Gulf Biologic Station for an intensive study of the shrimp; consequently these preliminary papers contain only brief observational notes on the behavior and a few scattered length measurements. Spaulding, whose observations were the most extensive, reports that larval shrimp, less than one half inch in length, were obtained in Calcasieu Pass in August and September. These were similar in form to the adult, but a series of larval stages was not obtained nor was identification of the species possible. No females with developed ovaries were taken, but from a study of the males and the time of appearance of the larvae he concludes that there is a single breeding season extending from the first of May to the last of July. He thought it possible that the eggs were laid in the Gulf but presents no direct evidence. The size at maturity is not established.

In 1918 the Louisiana Department of Conservation began a more intensive study of the shrimp. This work was done by Percy Viosca and published partly under his name (1920) and partly under that of Tulian, who was then commissioner (1920, 1923, 1926). Viosca's findings are more extensive than his predecessor's but it is to be regretted that none of the data upon which his conclusions were based is given in any of the publications. As a result it is impossible to evaluate his interpretations of the life history. He states that *Penaeus setiferus* spawns in the Gulf, chiefly on the evidence that sexually mature shimp are found only in outside waters. The young are said to live in the plankton of the Gulf until a size of 1¼ inches is reached. "By May reasonable numbers of baby shrimp appear in the shallow waters near the coast line and a large proportion gradually migrate into brackish water, all growing rapidly throughout the summer."

This is all the information toward a life history of *Penaeus setiferus* available in 1930.

The following is a bald summary of the life history as determined by the present work.

The eggs are laid from March or April to August or September in the outside waters of the ocean or Gulf. The post-larval young beginning at a length of 7 mm are found in bays, creeks, bayous, and lakes in warm, shallow, brackish water with mud bottoms. The young grow rapidly and with increasing size gradually migrate to deeper water of greater salinity.

During July at an average length of about 90 mm they enter the commercial catch, appearing first in the bays, creeks, and other "inside" waters and later outside.

They continue in the fishery, furnishing all of the fall catch, with its peak in October, until the following spring and summer, when they spawn and disappear at the age of 1 year. By late fall they have reached a length of about 120 mm, which they maintain during the winter. Resuming growth in the spring, they show a rapid and striking differentiation in the size of the sexes and spawn at lengths of 130 to 170 mm for the males and 135 to 190 mm for the females. Their fate is unknown, but their complete disappearance from the commercial catch is undoubted.

The breeding season is characterized by (1) a development of the gonads; (2) a rapid differentiation in size between the sexes; (3) a difference in the behavior of the

sexes, so that the proportion of sexes, uniform during the winter, shows wide fluctuation. Far more mature shrimp of both sexes are found outside than inside.

The shrimp is most abundant in shallow coastal waters near river mouths or deltas. It is omnivorous, feeding on a variety of animals and plants.

LIFE HISTORY

NATURE OF DATA

First in importance are the length frequencies obtained by measuring shrimp taken by the standard commercial gear, the otter trawl. All of the shrimp measured in Texas were samples from the catch of fishermen; the same is true of part of the data from Louisiana. The remainder of the shrimp were obtained with standard gear from boats operated by members of the staff in Louisiana, Georgia, and North Carolina. This experimental fishing differs from the commercial fishing solely in the localities fished. The fishermen obviously cannot afford to fish in localities yielding small catches, while in the experimental fishing these localities give information fully as valuable as those where many shrimp are taken. Of these length-frequency series the most important are those for *Penaeus setiferus*, although similar but far less complete data are available for *Penaeus brasiliensis*, *Xiphopenaeus kroyeri*, and *Trachypenaeus constrictus*. The series from Georgia is, because started earlier and unmarred by breaks, the most valuable.

The total length measured from the tip of the rostrum to the tip of the telson has been used as the standard measurement. This measurement was chosen over other linear measurements such as carapace length and over weight and volume after a study of the variability of measurements obtained in various ways. Weight and volume are subject to great variation because of the adhering water on a body as irregular in shape as the shrimp. These measurements consume much time and require apparatus not easily used aboard small boats. In obtaining the total length the shrimp is placed, ventral surface down, on the scale of a special measuring board with the rostrum in contact with a fixed block. The measurement is read and recorded to the nearest millimeter. For plotting and analysis the measurements are first tabulated, then grouped into 5-mm classes in such a way that the mid-point always falls on a 3 or an 8. For example, all shrimp measuring from 131 to 135 mm (both figures inclusive) are grouped together in a class interval with a mid-point of 133 mm and so plotted in a frequency polygon. Similarly, all from 136 to 140 mm are grouped with a mid-value of 138.

Measurements other than total length have been made for special purposes and in smaller numbers; most notable are those for racial studies now in progress.

The measurements from the four localities, covering, in the case of Georgia, over 2 years, now number more than 150,000 and therefore represent an adequate basis for statistical treatment. (See table 3.)

TABLE 3.—*Shrimp (Penaeus setiferus) measured during semimonthly periods in the three major regions of investigation*

Period	Georgia		Louisiana		Texas	
	Males	Females	Males	Females	Males	Females
1931						
Feb. 1	547	638				
Feb. 2	1,024	1,111				
Mar. 1	476	563				
Mar. 2	559	627				
Apr. 1	819	830				
Apr. 2	732	821				
May 1	1,222	1,314				
May 2	1,012	1,287	155	139	495	536
June 1	604	1,010			575	525
June 2	81	411	37	50	311	289
July 1	453	411			494	506
July 2	427	373	530	476	69	131
Aug. 1	918	521	969	788	222	178
Aug. 2	1,730	1,398	964	889	433	367
Sept. 1	1,531	1,467	1,906	2,004	315	310
Sept. 2	1,552	1,720	1,972	2,028	488	512
Oct. 1	684	752	1,151	1,308	598	602
Oct. 2	1,320	1,389	1,339	1,261	588	612
Nov. 1	632	679	1,994	2,206	394	406
Nov. 2	1,158	1,323	319	362	463	537
Dec. 1	1,737	1,862	349	451	439	561
Dec. 2					348	452
Subtotal	19,227	20,507	11,775	11,962	6,232	6,524

Period	Georgia		Louisiana		Texas	
	Males	Females	Males	Females	Males	Females
1932						
Jan. 1	456	529	328	317	178	222
Jan. 2	476	561			172	228
Feb. 1	301	343			777	823
Feb. 2	275	338			193	207
Mar. 1	507	514	485	607	291	309
Mar. 2	457	528	361	378	186	214
Apr. 1	1,260	1,322	272	265	420	480
Apr. 2	1,349	1,592	126	82	101	99
May 1	125	212	326	285	118	282
May 2	662	931	233	248	393	407
June 1	349	596	73	49	177	223
June 2	314	688	248	290	101	99
July 1	373	356	237	270	314	386
July 2	963	683	255	287	306	294
Aug. 1	1,017	704	217	204	792	608
Total	28,110	30,401	14,936	15,244	10,751	11,305

Beside length measurements, all observers have recorded the conditions of the gonads, permitting these specimens to be classified not only by length but also by stage of sexual maturity.

The field examination has been by naked eye, but in addition all the observers have made microscopic examination of part of the specimens and preserved material for future study as a check on the field classification.

Smaller shrimp than those taken by the commercial gear have been seined or taken by small beam trawls or "try nets" with bobbinet casings. These shrimp, ranging from 7 to 20 mm, have been measured under the low power of the microscope with an eyepiece micrometer.

Of a different nature is the material obtained by plankton nets. The study of the larval stages thus obtained is not yet complete.

INTERPRETATION OF DATA

RECOGNITION OF AGE GROUPS

The interpretation of the length-frequency data from Georgia upon which, as our most complete series, most of our knowledge of the life history is based, may conveniently begin with those for July 1931. Here there is a well-marked bimodality of the curve due to the presence of two completely separated groups differing markedly in size. This is plainly shown in figure 6, in which the smaller group with a mode at about 95 mm extends from 65 to 125 for both males and females, while the larger group, centered about 153 mm for the males and 175 for the females, extends for the males from 140 to 170 mm and for the females from 150 to 190 mm. There is thus a gap of 20 mm between the two groups. At no other time of the year can two completely separated groups be found. Examination of the other records show an essentially similar condition during July in Louisiana and during August in Texas.

Let us first trace these groups backward to see whence they come. In the case of the larger group this is easily done. Neglecting minor changes of size, this group can be traced back through the spring and winter to the previous year, where we may leave them for the present. (See fig. 10.)

The smaller group is less easily followed. They are not present in the commercial catch in the earlier months. An extensive search for this group of young has been carried on by seining in shallow water, representing many degrees of salinity,

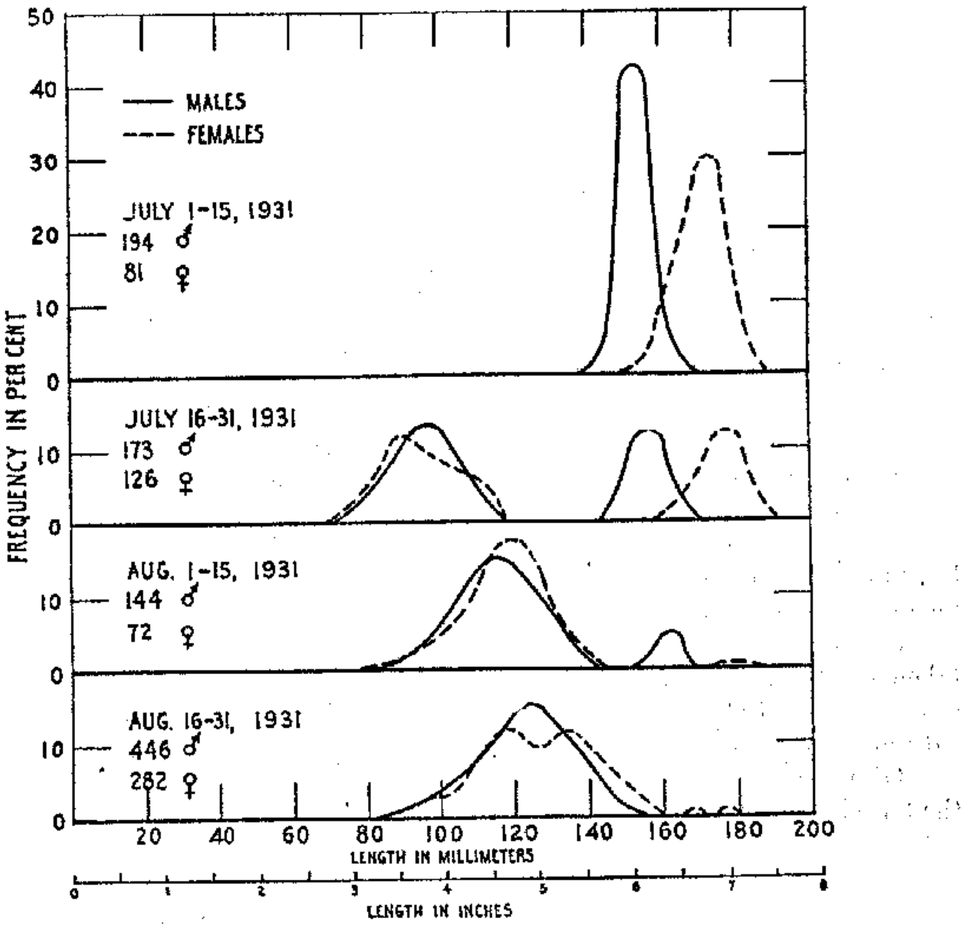

FIGURE 6.—Half-month frequency distributions of the common shrimp from the outside waters of Georgia, July 1 to August 31, 1931, showing the first appearance of the young shrimp of the year and the disappearance of the mature shrimp from the commercial catch.

from ocean beaches to creeks and lakes far inland. Many localities yielded nothing. So far no young have been found on ocean or Gulf beaches either in Georgia, Louisiana, or Texas. In the marshes near the grass small shrimp were taken but proved to be young and adult palaemonids. Finally, in the summer of 1931, the young were found in the slightly brackish waters of Dover Creek at Lampadozier, Ga., 10 or 12 miles from the sea. Here the young from 7 or 8 to 40 mm have been systematically collected during the proper seasons.

In Louisiana during 1932 the young have been obtained under a variety of conditions ranging from the slightly brackish waters of Bayou Rigaud in lower Barataria Bay to the almost fresh waters of Little Lake. The latter is more than 20 miles

distant from the Gulf in a direct line and much farther by the winding bayous and canals through which the shrimp would have to pass if, as seems probable, they were spawned at sea. Also during 1932 these young shrimp have been found in similar localities near Beaufort, N.C., and Aransas Pass, Tex., consequently records are now on hand for these young from the four States in which the investigations are in progress. The habitat of the post-larval young up to about 50 mm seems to be on the inside and appears to be characterized by shallow water, muddy bottoms, high temperature, and moderate to very low salinity. A more detailed study of the physical characteristics of the localities in which young shrimp are found is in prog-

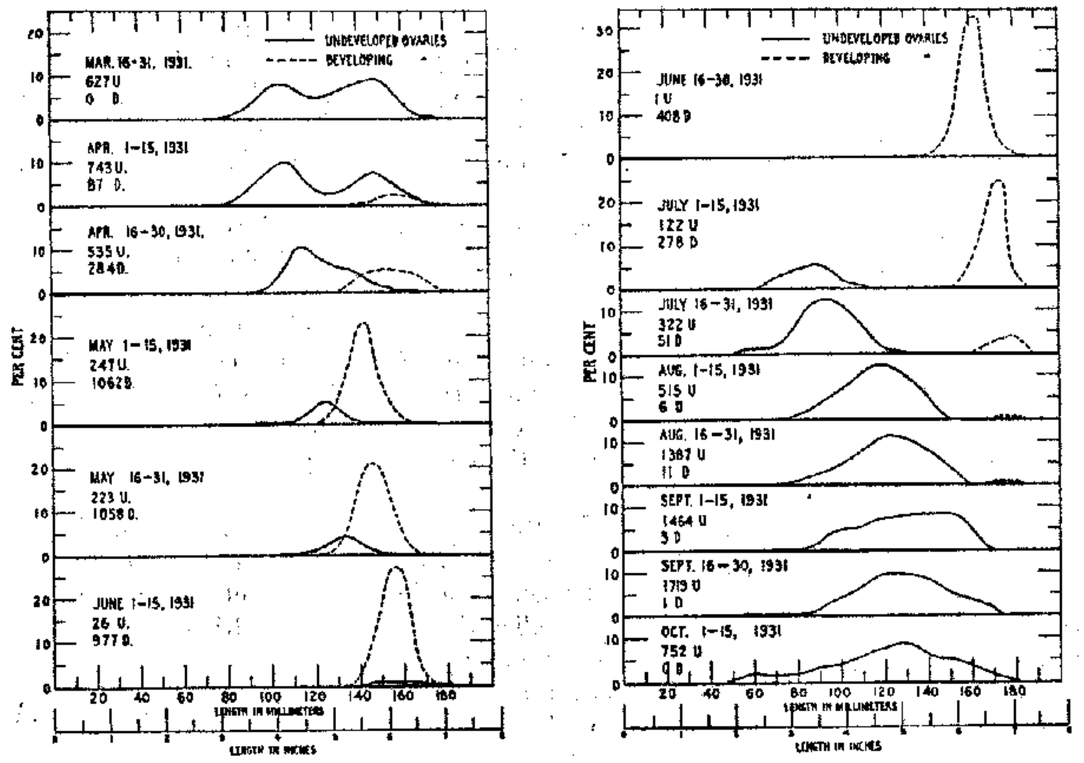

FIGURE 7.—Frequency distributions of the immature and maturing females of the common shrimp in Georgia waters during the spawning season of 1931. Solid lines represent distribution of female shrimp with ovaries composed exclusively of undeveloped eggs and broken lines indicate distribution of shrimp with maturing eggs.

ress. These bayous, creeks, and lake margins are also nursery grounds for many species of fish, the larvae and young of which are taken while seining for the young shrimp. While *Crago*, the shrimp of the North Sea, differs in many respects from *Penaeus*, the young also make their early growth far from the sea (Ehrenbaum 1890).

SPAWNING

What is the origin of these very young, apparently just emerged from the larval state, some of which can be found from April through September? We naturally turn to the larger group which we have said was present at this time. If we classify the large shrimp by the observed state of the gonad, we have the following picture. In Georgia, in 1931 from the middle of April to the end of July, some degree of maturity was observable in the ovaries. The members of the small group appearing in July were without exception immature. Some scattering representatives of the

larger mature group were found in August and even September, but the score of individuals taken are in striking contrast with the hundreds obtained in earlier months.

Although we have distinguished four or five stages of ovary development in our records, it is difficult to separate these sharply or to determine how long each lasts. Judging from the appearance of the ripest stages that we have recognized and of the young, some shrimp are spawning within 2 or 3 weeks from the date on which ovary development is first noticed. We may say, therefore, that in Georgia in 1931 the larger group was spawning from the last of April to the middle of August and that the young entering the commercial catch in July came from the earlier spawners among these large shrimp. The intervening time had been spent by the young probably in the smaller and more brackish creeks in feeding and growing.

Having thus established the previous history and relations of the two groups found in the commercial catch of July, we may profitably complete the presentation of all the data on breeding and spawning that we have obtained. Like Ehrenbaum in his work on *Crago vulgaris*, we must confess to serious gaps in this phase of the life history.

The *Penaeidae* as a group are characterized by marked sexual dimorphism, including certain elaborate and well-marked secondary sexual characters associated with sperm transfer.

In *Penaeus setiferus*, in contrast to the crabs, the female is much larger than the male. Thus, in Georgia, in June 1931, males and females of a comparable degree of maturity averaged 144.5 and 156.5 mm, respectively, the females thus exceeding the males by 8.31 percent. There are other differences in general form; according to Alcock (1906) the rostrum of the female is proportionally larger, a persistent juvenile character.

The most interesting differences for the question that we are now considering are those of the secondary sexual characters. In *Penaeus* the males produce spermatophores, often of considerable complexity. The inner ramus of the first pair of pleopods is modified, forming a structure called the petasma or andricum. By means of the petasma the spermatophore is presumably transferred to the female, although the process as far as we know has never been observed. In *Penaeus setiferus* the endopodite of the second pair of pleopods is also modified to some extent and probably also plays a part in the transference of the spermatophore.

In most species the female has on the ventral surface of the thorax between the bases of the last pair of pereiopods a structure of plates partially enclosing a space into which the spermatophore is placed. This thelycum varies greatly in complexity, in some species (*Penaeus brasiliensis* and *Xiphopenaeus kroyeri*) being well formed, in others less developed.

In *Penaeus setiferus* the thelycum is vestigial in character and does not function as a secondary sexual organ. The spermatophore is attached, by a gluelike secretion of the male, to the ventral surface of the female between the bases of the third and fourth pereiopods. Two winglike processes on the anterior end of the attached spermatophore fit securely into the grooves between the third and fourth pereiopods and form an inverted funnel into which the "glue" flows, fastening the spermatophore to the female.

The spermatophore so attached is quite easily dislodged. This may, to a certain extent, explain why in *Penaeus setiferus* spermatophore-bearing females are much less abundant in the catches than are similar females of *Penaeus brasiliensis* and

Xiphopenaeus kroyeri. In fact, only 20 such females have been obtained from the thousands of shrimp examined. Considering only females handled during those months in which spermatophores have been found, we have the relations shown in table 4.

TABLE 4.—*Penaeus setiferus spermatophore records April to August 1931 and April to July 1932*

State	Females examined	Spermatophores found	Percent
Georgia	11,015	3	0.027
Louisiana	3,561	7	.20
Texas	3,911	10	.26

All these 20 spermatophore-bearing females were in the ripest of the stages distinguished by examination of the ovary. Their lengths, which range from 141 to 186 mm with a mean at 166.3, agree well with the lengths of females showing the last stages of maturity.

The period in which these females are found is from April to August, inclusive, which covers almost the entire season during which the ovaries appear ripe. All were taken in fairly deep water, either in open sounds or the sea or Gulf, in localities where the salinity is the highest found in the range of the shrimp for this season of the year.

The next question is as to the time during which the male is capable of furnishing spermatophores. The spermatophores when formed are easily recognized in, or expressed from, the lower end of the vasa deferentia of the male, and records of their presence or absence are at hand for part of our series of length-frequency data. In 1932 in Louisiana maturing males were first present in the latter part of March, thus appearing slightly in advance of maturing females. They usually appear slightly earlier and last as late in the season as mature females. We may conclude, therefore, that during the period that females are capable of spawning, breeding males are also present.

To summarize: Ripe females are common during April, May, June, July, and present but scarce in August and September (Georgia, 1931). Spermatophore-bearing females have been obtained from April to August (these must be within a few hours of spawning). Mature males are present throughout this period. Young in the first post-larval stages are found from at least late April to August. We feel justified in assuming, on the basis of these data, that in 1931 spawning occurred during April, May, June, July, and to a reduced extent in August and September, even without having as yet observed spawning or having obtained fertilized eggs. Of course, the dates of spawning will vary from season to season.

It may next be inquired, Where are the shrimp spawning grounds? On this important question our evidence is again indirect, consisting of four types of data—the relative distribution of males and females, the relative distribution of the various stages of maturity, the distribution of that stage of maturity represented by the spermatophore-bearing females, and the distribution of larvae.

The plankton material containing penaeid larvae has not yet been analyzed and therefore cannot throw light on the location of the spawning grounds.

As stated, all spermatophore-bearing females have been obtained in fairly deep water of high salinity. Since we have good reason to think that the spermatophores

are soon dislodged and the eggs must be laid and fertilized before this happens, we may infer that spawning occurs in these localities.

There remains to consider the distribution of the sexes and the stages of their maturity. As the simplest we shall first consider the distribution of the stages of sexual maturity. If the numbers of immature and maturing males or females from different localities are compared, the greater proportion of maturing individuals will be found in outside waters. (See fig. 8.) This is more marked with the later stages of maturity. Thus, in Georgia, in 1932, an intermediate stage of ovary development was over twice as common in outside waters as in the creeks, while the last stage of ovary development recognized was six and one half times as common. As will be recalled, the spermatophore-bearing females, which represent the last stage of maturity, were all found in the Gulf or ocean with a single exception taken in an exposed sound. A satisfactory analysis of these data will require the inclusion of figures from another breeding season and must be presented at a later date. The present data can be interpreted in but one way—that by far the greater proportion of spawning takes place in the Gulf or ocean and that only a slight amount, if any, occurs on the inside. The spawning seems to be correlated with high salinity.

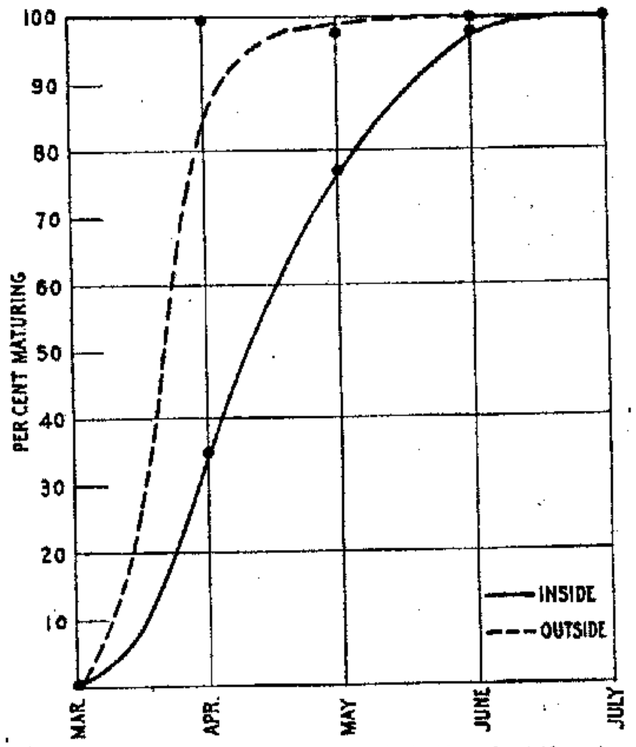

FIGURE 8.—Percent of maturing females in the inside and outside waters of Georgia from March to July 1931.

SEX RATIO

A comparison of the proportion of the two sexes in the catch at different times of year and in different localities shows fluctuations associated with spawning. Since additional data will be required for a satisfactory analysis of these fluctuations, only brief mention of the facts will here be made. As may be seen from figure 9, in Georgia from February 1931 to July 1932 there is a well-marked annual cycle. During the winter (from the last half of September 1931 to the last half of April 1932, inclusive) the proportion is constant, the females constituting slightly over 52 percent of the 25,601 shrimp measured. During the similar part of the preceding year the females furnished essentially the same proportion of the 11,283 shrimp. In contrast, the period from the last half of May to the first half of September 1931, inclusive, and again from the first half of May to the first half of August 1932 (where, at this time, our record ends) there are sudden and remarkable fluctuations of the proportion, the females rising above 80 percent and falling nearly to 30.

This period covers the time during which the adults mature, spawn, and disappear. A few weeks after spawning begins and when about half the females are maturing the fluctuations begin and only end with disappearance of the adults from the fishing. The rise in proportion of the females succeeded by a fall appear to be the result of differential behavior of males and females associated with spawning. We have found no indication of a sex reversal in *Penaeus* such as has been claimed by Berkeley for *Pandalus*.

Further data is being collected on this interesting question.

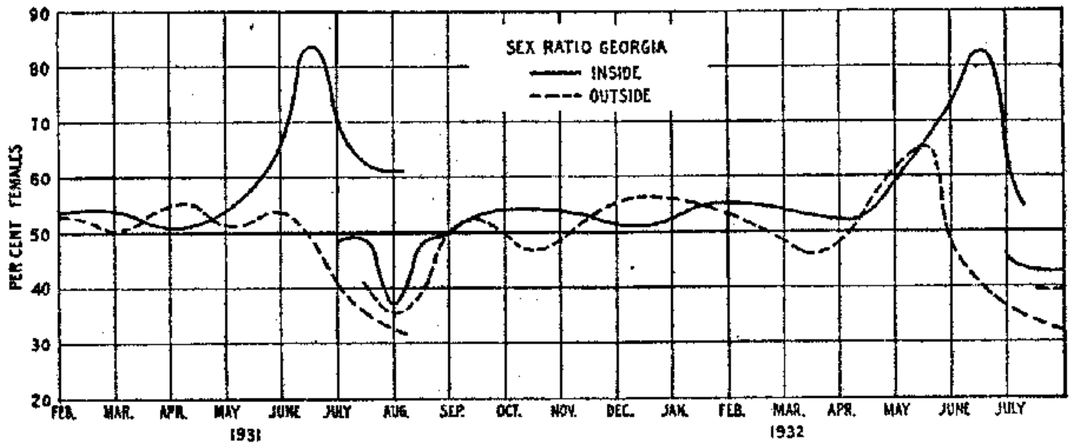

FIGURE 9.—Percent of females appearing in catches from inside and outside waters of Georgia from February 1, 1931, to August 15, 1932, during which period 58,521 shrimp were measured and examined.

LARVAE

The study of the larvae of *Penaeus* by Müller (1863, 1864), Brooks (1883), and Kishinouye (1900b) have shown the main features of the unusual larval history beginning with the nauplius, not found elsewhere among the higher crustacea. There are a large number of stages (6 to 8) including nauplius, metanauplius, protozoea, zoea, metazoea, and mysis. In no case has the species of the larvae been known with certainty, and in consequence there exists no data for the identification of the larvae. This is a serious lack where 4 species of penaeids appear in the commercial catch and 15 or 20 have been recorded, the larvae of which may be encountered. Other facts indispensable to this phase of the life history, such as the duration of the stages and their behavior, are also lacking.

The extensive plankton collections of the investigation have not yet been studied in detail, and although larvae are present we are as yet unable to give a satisfactory summary of their distribution.

YOUNG

From the distribution of the mature adults, spawning must take place predominantly, if not exclusively, in outside waters of high salinity. What little is known of the distribution of the larvae does not conflict with this. The distribution of the post-larval young is, however, different. These forms, essentially similar to the adult except in size, the smallest that we have obtained measuring 7 mm in length, give up the swimming habitat of the larvae and seek the bottom, thus resembling the adult in habits as in form. The young, as has been stated, are found on muddy bottoms in shallow water of high temperature and low salinity exclusively in bays or inside waters and often far from the ocean or Gulf. The upper limit of size of the young in

this habitat is not sharply defined; some shrimp as large as 100 mm have been encountered, but the majority are below 40 mm.

We have no data on the growth in this earliest stage, but they first appeared in the Georgia commercial catch at an average size of 90 mm (70 to 105) in July 1931, and again in July 1932, 2 or 3 months after the beginning of spawning. The reactions that lead the larvae from the outside more saline waters to the brackish muddy-bottom waters favored by the young, or lead the young back to the waters of higher salinity where they first enter the commercial catch, have not been studied, although they must hold the key to an understanding of one of the most interesting phases of the shrimp life history.

To compare with this picture just given of the spawning, larvae and young of *Penaeus setiferus*, we may review the findings of Ehrenbaum (1890) on *Crangon* (*Crago*), Mortensen (1897) on *Palaemon*, and Kishinouye (1900a), Spaulding (1908), Gates (1910), and Viosca (1920, Tulian 1920, 1923, and 1926) on *Penaeus*. Ehrenbaum found that in the North Sea the ovigerous females of *Crago* and the small free swimming larvae are found only in the strongly salt water of the flats and about the offshore islands of the North Sea. Only very exceptionally are larvae or ovigerous females taken in the brackish waters of the estuaries.

In sharp contrast, the young, measuring 5 to 10 mm, are found in great numbers from spring to late summer in the Dollart and Jade Rivers, far upstream in brackish water. From the percentage of ovigerous females found at different seasons, Ehrenbaum concluded that there were two spawning seasons and that hatching occurred primarily in July and to a less extent in March. No additional support for the double spawning season has been presented by the later writers.

In *Palaemon fabricii*, studied by Mortensen, the females spawn in deep water in May, the eggs hatching chiefly in June. As in *Crago* the larvae are pelagic and never appear in the brackish water of fjords or creeks. After a pelagic life of 3 to 5 weeks, the first young appear early in July. The young are found in the rapidly growing vegetation of the shallow water of little creeks and fjords. The larger females are said to lay a second batch of eggs shortly after the hatching of the first. In neither of these species has fertilization been observed.

It will be seen that the distribution of the ripest females, the larvae, and the young in both these species agree with what we have observed in *Penaeus*.

The data of Kishinouye (1900a) are of more interest because they deal with various Japanese species of *Penaeus* closely related to the forms we are studying. Unfortunately, the basis of his statements are not given in the English summary of his paper. He gives tables for sexual maturity in five species. The period of May to September, inclusive, contains all these mature seasons, although most are individually shorter than this. In three species the males are said to be sexually mature throughout the year. The eggs ripen in spring and spawning takes place in summer and autumn. Kishinouye describes the spermatophores in several species. Eggs are said to be discharged from time to time as they ripen. He mentions finding the larvae in shallower water than that in which the spawning shrimp live but does not specifically describe the habitat of the young.

The breeding season given by Kishinouye agrees in general with our findings. It is not true of the male of *Penaeus setiferus* that mature individuals are present at all times of the year, as he claims for certain species. We are very much inclined to doubt that in *Penaeus setiferus* spawning takes place from time to time as the eggs ripen; it is more likely that all the eggs are spawned at one time.

Only those findings of Spaulding, Gates, and Viosca relating to the spawning and young will be given here. Spaulding thought that the breeding began about the middle of June and that spawning took place "in the deeper water of the larger bays or even in the Gulf." He interpreted his data as showing either a long breeding season during the summer or two breeding seasons a year. Two years later (1910) Gates reported that there was only one breeding season and that "this extends from, approximately, the first of May to the last of July." Our investigations show that the period given by Gates covers the most intensive portion of the spawning season and that the entire season may be longer by a month or two on either end. Contrary to Gates' assertion that "the smaller the shrimp the earlier it spawns", we find that the larger shrimp mature first, consequently they also probably spawn first (fig. 7).

Viosca states that *Penaeus setiferus* spawns in the Gulf, chiefly on the evidence that sexually mature shrimp are found only in outside waters. The young are said to live in the plankton of the Gulf until a size of 1¼ inches is reached. "By May, reasonable numbers of baby shrimp appear in the shallow waters near the coast line and a large proportion gradually migrate into brackish waters, all growing rapidly throughout the summer."

That the sexually mature shrimp are more abundant in the Gulf than in the inside waters agrees with our experience, but that no mature are taken in the bays is too sweeping a statement. Although always strikingly less abundant, especially in the more mature stages, we have records of many shrimp in advanced stages of ovary development from the inside waters both of Louisiana and of Georgia.

Viosca was led, apparently, to infer that the larvae live in the plankton up to a length of 1¼ inches by his inability to obtain smaller young. The largest larvae found by Müller were 4.5 mm long, the smallest post-larval young about 5 mm. We have obtained young as small as 7 mm. Obviously the larvae do not reach a length of 1¼ inches (31.75 mm). Either this size was inferred but not actually seen, or, if seen, some other crustacean was mistaken for *Penaeus*. We have been unable to find young of this size on the outside, either in the plankton, the trawl material, or on the ocean beaches, although we have obtained them in inside waters in all four States in which we have worked.

Although a gradual inward migration of young such as pictured by Viosca would be a reasonable process, the presence of many young of 7 mm and up in the creeks, bayous, and lakes, and their complete absence on ocean beaches show that the larvae often pass directly to shallow brackish waters. Like Viosca we have found that the larger young of 20 to 50 mm move, in general, seaward through the summer and fall, so that there is always a gradient of decreasing size from the waters of greater salinity toward fresh water.

Owing to the extended spawning season, the advent of the young into the commercial catch is followed week by week by new contingents which move into the fishing zone and become large enough to be taken by the trawls. As a result, the lower limit of size in the commercial catch is approximately constant through the summer and into the fall, as might be expected, since the limit is set by the selective action of gear and the movements of the young and not by growth. It may be affected, however, in a minor way by changes in temperature or by changes in the fishing areas which are not always strictly comparable from month to month.

GROWTH

Because of the fact that young are constantly being added to the population sampled by the fishing, it is extremely difficult to approximate the growth. As the earliest spawned shrimp continually increase in length, and small of a relatively uniform size are constantly appearing, the range of sizes, of course, increases; consequently the growth is not represented by the mean or modal lengths, which each month are based on a new assortment of ages. It is clear that the increase of the means is much slower than the growth of shrimp of any particular age.

The advancing upper size limit of the entire group should measure the growth of the older shrimp but is difficult in practice to determine. No statistical measure exists which will be comparable for all these types of compound frequency curves. In discussing the series of length frequencies, we have used the mode, or most abundant size as determined by inspection, for the average, and for the upper and lower limits a point where the ordinate has fallen to 1 percent of the total number of measurements. Admittedly inaccurate, this may serve, however, as a first approximation for the purposes of the present discussion.

The length-frequency data obtained with a standard trawl in the ordinary fishing grounds is ill adapted to show growth. For the present, therefore, only the most general features will be sketched and a more detailed analysis postponed to a future time when another season's records are available.

The average size of the young at the time of appearance in July 1931 was about 90 mm, with a range from 70 to 105. (See fig. 10.) At this time there is no significant difference in size between the sexes; in fact a clear differentiation does not occur until the following April. Through July and August growth is rapid; and by the 1st of September the most common size is about 130 mm, while the largest exceed 160 mm. The lower limit rises slightly and remains at approximately 80 mm until the first of the following year. We may consider that with the present gear about 70 mm is the minimum size entering the commercial catch to any extent.

During September, October, and November the average length fluctuates between 120 and 130 mm. During this period the females seem slightly the larger. This is the time of the fall maximum of abundance and the peak of the average commercial catch. From a value of 130 mm early in November the average size falls slightly, reaching a low point of about 120 mm near the first of the year. The difference in size between the sexes also disappears. This corresponds in a general way with the low period of the commercial catch.

Obviously these decreases of average size must result from behavior, which is differential with regard to size—the large and the small shrimp must frequent different localities or react differently in other ways. It is suggestive that the winter decrease of size is accompanied by a very marked decrease of abundance. During the low temperatures of the winter, movements or habits of the shrimp are changed in such a way as to remove the majority of them from the field of the commercial fishery on the Georgia coast.

Following the first of the year (1932) the lower limit begins slowly to rise and by the 1st of April has increased from 80 to 100 mm. It is apparent that by January the last shrimp spawned in the preceding summer have entered the commercial catch and that the increase of the lower limit now reflects the growth. This seems the more probable, since the average advances at the same rate from 120 to 140 mm during this time.

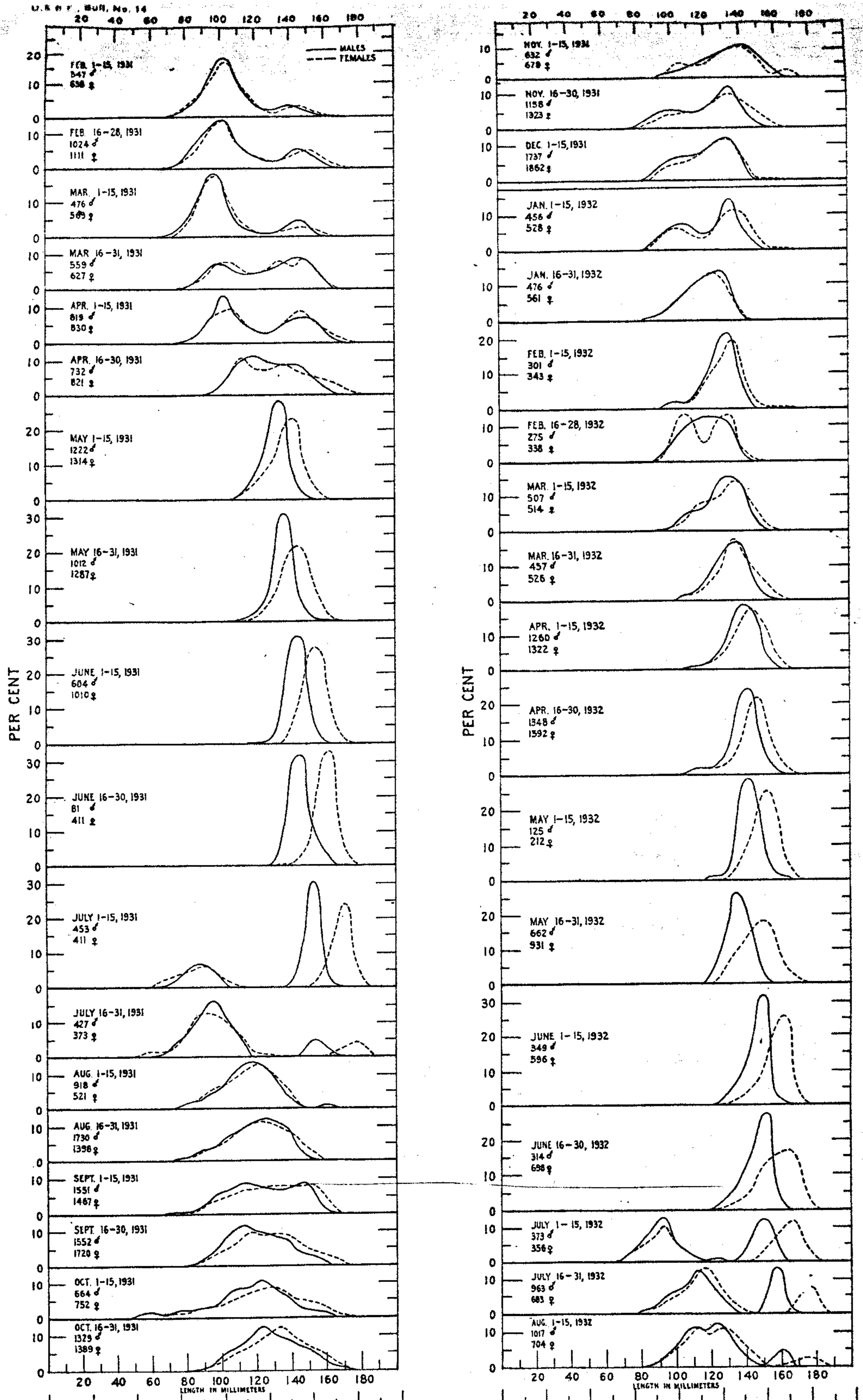

FIGURE 10.—Frequency distribution of the population of common shrimp in half-month periods for Georgia from February 1, 1931, to August 15, 1932. These curves represent the measurements of 58,521 shrimp. With but few variations the distributions for Louisiana and Texas follow those for Georgia very closely.

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During the following months of April, May, June, and July 1932, accompanying a steady increase of water temperature from 56° F. in March to 86 in July there is a remarkable exhibition of growth. This is manifested in three ways. The steady ensuing growth is differential, being more strongly expressed in the females than the males; there is a surprising reduction of the size range; and the sex products mature rapidly.

As will be recalled, this period coincides with the time during which mature shrimp are taken. These first appear among the largest; but soon the smallest have exceeded the minimum size for sexual maturity, maturing becomes general, and by the 1st of July no immature of any size can be found in this group of shrimp.

The progress of growth is very interesting. During the spring, in each sex a distribution of wide range without a sharp mode is converted into a compact group with little variation of size and a well-marked mode. This may be caused by either or both of two processes—first, the more rapid growth of the smaller and younger members; second, the disappearance of the larger individuals that have spawned. Whatever the process, its orderly progress is striking. In fact, a frequency distribution from May or June may readily be identified by its characteristic shape.

Although up to April there has been no significant difference in size between the sexes as evidenced from the frequency curves (except for the short period in the fall of 1931 already noted), the growth of the females, beside producing a characteristically compact and homogenous group of this sex, rapidly outstrips that of the males until in June, as previously stated, the sexes differ in length by 8 percent, the males averaging 144 and the females 156 mm. By this time the range has been so reduced that the ninth decil of the males (the largest males remaining after the upper 10 percent have been cut off) is below the average of the females and the first decil of the females is above the average length of the males.

FATE OF ADULTS

A question of great interest and importance both from the theoretical and the practical standpoint is the fate of the larger group present in July. The smaller group of shrimp, traced into earlier months, was found to have been spawned by the larger, and the larger to have overwintered from young of the previous spring or summer. Traced onward from July the smaller group persists through the winter and spawns the following spring and summer. Does the group of larger shrimp also survive the winter and take part in a second spawning?

Again our evidence is indirect but impressive. We shall consider the length frequency and sexual maturity data in the light of the abundance of the shrimp. No accurate measure of the abundance of the shrimp in the waters of Georgia at different seasons is available. An approximation, however, is furnished by the number of shrimp taken in experimental trawling. By these useful, although imperfect, data let us follow the abundance of the group of small shrimp from the time of their entrance into the commercial catch until their disappearance. The numbers increase rapidly, being constantly augmented by new young of later and later hatchings. The maximum of abundance is reached in the fall, usually September or October, agreeing in time with the fall peak of the commercial catch. (See fig. 11.) Although the fall peak of the total catch tends to be overemphasized by the intensity of the fishing at this season and in general economic factors prevent a complete correspondence, nevertheless the fall catch rests on a period of marked abundance of shrimp. From

this peak the abundance declines and reaches a low point in late winter and early spring, coinciding with the low point of the catch which falls in February, March, or April.

The numbers obtained by experimental trawling then again increase, reaching a second peak in April or May at the time of the spring catch of large, mature shrimp so prized by the canners. The crest is more prominent and earlier than the spring catch would suggest.

From this peak of abundance there is a rapid and steady decline. In the first half of July, when the young of the year make their first appearance in the commercial catch, the two groups are approximately equal in abundance. By the latter part of the month the abundance of the group of larger shrimp has already fallen

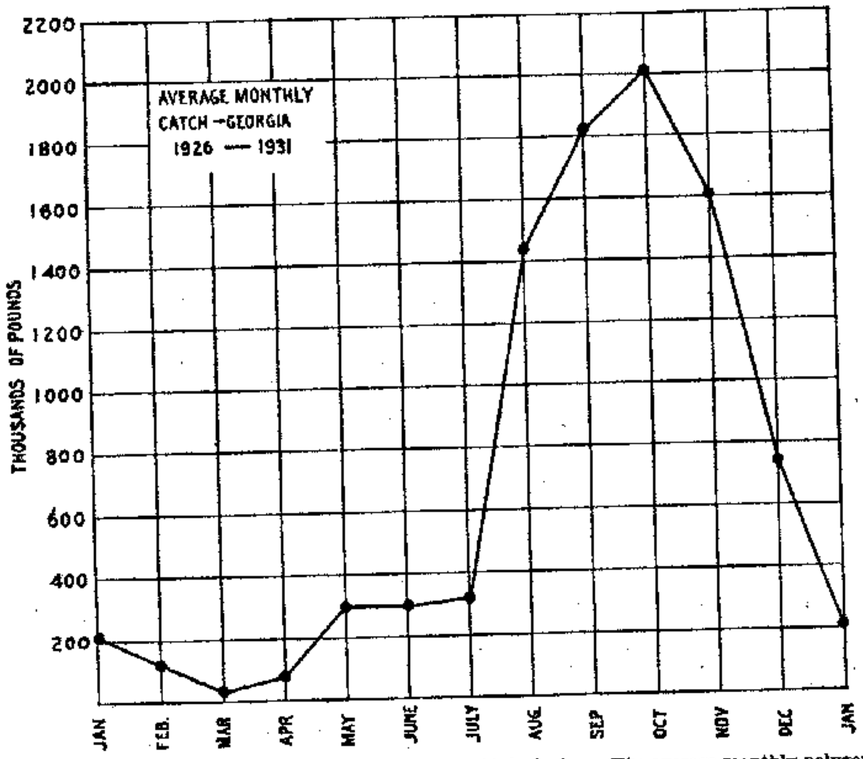

FIGURE 11.—Average monthly shrimp catch in Georgia from 1926 to 1931, inclusive. The average monthly polygons for Louisiana and Texas follow the Georgia polygon very closely.

below that of the growing young. The group of large shrimp can be more or less clearly recognized in August by their greater length, but the rapid growth of the young (see fig. 10) soon brings about an overlap, so that size alone will not suffice to identify them. The group of large shrimp are at this time sexually mature, and by this criterion a few may be found in September, but the number is very small—two or three out of hundreds. A careful study of the size frequency curves and those of sexual maturity fail to disclose further trace of them, and we are forced to conclude that they disappear from the fishery in Georgia. We have also been unable to find spent individuals such as should be present after the spawning season if the adults remained within the range of the fishery. Among the thousands of immature shrimp no undoubtedly spent female has been found, although some males examined may possibly belong to this category; the number of these, however, is small.

Kishinouye (1900a) believes that certain species of *Penaeus* die after spawning while others live through a second year. He does not indicate the basis of this belief.

Without evidence, it is idle to speculate whether the process of spawning is fatal to the shrimp—whether, like the salmon, they are weakened and soon succumb to enemies and disease or whether they retire to some new and as yet undiscovered habitat. All we know is that they play no further part in the fishery. The shrimp is therefore an "annual", being spawned in the spring or summer, spawning at the same season of the following year, and then passing out of the fishery. Since it is probable that those spawned early furnish the early spawners of the next year, the life span is very close to 1 year. This is the condition in Georgia. Whether or not in Louisiana and Texas the life span will prove to be the same is not yet settled, but the data so far available give no evidence of an essentially different life history.

It should again be emphasized that the above account refers only to *P. setiferus*. How many of these findings may apply to *P. brasiliensis*, *Xiphopenaeus kroyeri*, and *Trachypenaeus constrictus* remains to be determined. A consideration of these forms has been deferred because of their lesser importance and because data on these less common species has accumulated far more slowly.

HABITS

Observation of the shrimp under natural conditions is so difficult that only the most obvious habits can be thus determined. Systematic observations in aquaria have not yet been carried out. In spite of the paucity of direct observation it may be well to assemble what general knowledge is available. As already stated, *Penaeus setiferus*, like other penaeids, is a shrimp of subtropical littoral waters. The range of temperature under which we have taken it is 9° to 31° C. (48° to 88° F.). In the colder waters of the North Sea in Europe or of Alaska no penaeids are taken, the fishery depending rather on pandalids or cragonids. As with the Indian species observed by Alcock, *P. setiferus* appears to favor the deltas of large rivers like the Mississippi, although it is not confined to such localities. For example, shrimp are taken in large numbers off Cape Canaveral, Fla., in a region where there are no large streams. Perhaps the relation to rivers rests on the fact that, as we have seen, the young for part of their development frequent brackish or almost fresh water.

It appears to be more common on muddy than on sandy bottoms, but it must be remembered that mud is more common than sand in the neighborhood of large deltas.

Like other shrimp, *Penaeus setiferus* swims in two ways. Usually it swims forward by means of the pleopods or abdominal legs. When moving rapidly it swims or rather leaps backward by flexing the powerful muscular abdomen and sweeping the large tail fin under the body. In this way it may leap out of the water like a fish or out of an uncovered aquarium.

Although the shrimp spend most of their time on the bottom, there are a few well-authenticated cases where a school has been seen swimming near the surface. At times they bury themselves in the mud.

No systematic examination of the stomach contents has been carried out, but a few observations indicate that it is a voracious and well-nigh omnivorous feeder. This is supported by the observation of Viosca (Tulian 1920), and of Alcock (1906) and Kishinouye (1900a) on other species. Worms, crustacea (not excluding shrimp of the

same species), small mollusks, and plant debris are all eaten. Often it appears to eat the mud or sand for the organic matter which it contains. The presence of considerable amounts of mud or sand in the intestine appears to be the rule. In aquaria, fish or other shrimp are readily and successfully attacked and eaten.

Convincing evidence is at hand that the behavior of the shrimp is influenced by temperature and salinity, but as yet no observations have been made on its reactions to these stimuli or to others such as light, hydrogen-ion concentration, and oxygen tension. Early work on these important features of the shrimp's behavior occupies a prominent place in the program of the cooperative investigation.

DEPLETION AND PROTECTION

The shrimp investigation was initiated by the Federal and State Governments to supply the biological information necessary to guide analysis of the state of the fishery and to permit the framing of effective protective legislation when such is needed. It is not possible here to discuss in detail the bearing of the facts presented in this report upon the questions of depletion and protection; the intention is to do this in a subsequent publication. Here we may only indicate the lines which such a discussion must take.

First, it should be emphasized that depletion can only be detected by a careful analysis of the abundance of shrimp and that knowledge of abundance requires adequate statistical data. Existing catch statistics are inadequate, since they do not show the effort by which the indicated total catches were obtained. In addition we must know the amount of gear and number of men, or the individual boat catches must be recorded for analysis. Improvements in the method of gathering statistics have recently been made by Louisiana, and it is to be hoped that all of the eight South Atlantic and Gulf States will so modify their regulations covering the reporting of fish taken as to make possible the future analysis of abundance.

Fortunately it is not necessary to take an alarmist attitude, as we have obtained no evidence of serious depletion. At the same time common prudence should make impossible a complacent inaction until depletion is easy to see and hard to remedy. While there is yet time a concentrated effort should be made to institute the collection of statistics which may be used effectively in the immediate future.

In the absence of evidence of serious depletion at the present time we are unwilling to urge increased stringency of existing regulatory measures. We shall therefore merely suggest the bearing of the facts of the life history of the shrimp on the problems of protection and indicate the types of restriction which may be employed when analysis of the catch statistics indicates that additional protection is needed.

The outstanding features of the life history of the shrimp which may affect the question of its resistance to overfishing are: (1) Its short life span of 1 year, (2) its extended breeding season of about 5 months, (3) the very large number of eggs produced, and (4) its extensive habitat in the littoral waters of the South Atlantic and Gulf.

The shrimp's life span of 1 year, shorter than that of any other important economic animal, is clearly an unfavorable factor. The shrimp fishery must obviously lack the stability shown, for example, by the halibut fishery, where animals from 7 to 20 years of age appear in the catch and the entire failure of the young of any particular year would not seriously reduce the total. When the pressure of over-

fishing begins to be felt the shrimp will show sudden and violent fluctuations probably disastrous to the fishery.

Its extended breeding season of at least 4½ months, longer than that of the majority of animals of economic importance, and the large number of eggs produced are factors very favorable to the shrimp, since they render almost impossible the failure of an entire breeding season.

The South Atlantic and Gulf coasts, cut by a multitude of tidal rivers and bayous, furnish an unequaled extent of shallow, littoral waters of all degrees of salinity in which the shrimp flourishes. This extensive favorable habitat and the wide range extending from Massachusetts south to Brazil is an obviously advantageous condition. Without it, the multitude of shrimp would not have developed in this region. But while it may furnish a breeding reserve in places not readily fished, it affords no complete protection. The shrimp seems to be confined wholly to a narrow coastal strip favorable for fishing, since, as we have seen, *Penaeus setiferus* appears to be absent from deeper water. Certain of the creeks and bayous in which the young are found are unsuitable for fishing; but since these young all move to the larger bays or to outside waters during the winter, at some time all shrimp on our coast must run the gauntlet of trawls and seines. The number that escape depends wholly on the intensity of the fishery.

It is clear that under natural conditions the favorable factors were so far in the ascendancy as to produce an amazing abundance of shrimp. Even the great numbers taken by man have not sufficed to produce an alarming depletion. We must look forward, however, to a time when the increasingly intense fishery will turn the balance against the shrimp. Then the catch, maintained by constantly increasing effort, will begin to show great variations from year to year, some of them ruinous to fishermen and canners.

When additional protection becomes necessary it may take one or more of four lines—limitation of sizes taken, closure of certain seasons, closure of certain areas, and regulation of gear. All of these have been tried; the regulation of gear and the closure of certain areas, as, for example, nursery grounds and inside waters furnishing a preponderance of young, and certain seasons promise the most satisfactory results. Experiments now in progress will, it is hoped, indicate how gear may advantageously be modified.

SUMMARY

The present paper contains the results so far attained in certain phases of a cooperative program of study of the shrimp initiated by the United States Bureau of Fisheries and participated in by the States of Louisiana, Georgia, and Texas.

The shrimp supports the most valuable fishery in the South. Little has been known of its abundance, life history, and habits, consequently it warrants an investigation of some magnitude.

The importance of the shrimp fishery may be seen from the fact that in the United States in 1929, 113,263,000 pounds were caught, the value of which to the fishermen was $4,575,000. Of this, 95 percent was produced by the eight South Atlantic and Gulf States, Louisiana alone contributing 43 percent. In the South the shrimp exceeds the combined value of the two fisheries next below it.

Otter trawls operated from gas-driven boats take about 90 percent of the shrimp, the remaining 10 percent being caught by seines and cast nets.

Of the six species of shrimp caught in the South the common shrimp (*Penaeus setiferus*) is the most valuable. This species comprises about 95 percent of the catch in the South Atlantic and Gulf States, or about 90 percent of the entire amount of shrimp taken in the United States.

P. setiferus spawns from March or April to August or September apparently in the outside waters.

The post-larval young, measuring from 7 or 8 mm up, are first encountered in bays, bayous, and "lakes", sometimes far inland, but not on ocean or Gulf beaches. Their habitat is warm, shallow, brackish waters with muddy bottoms.

The young grow rapidly, and as they grow they seek deeper waters of greater salinity. During July, at an average size of about 90 mm, they enter the commercial catch, first on the inside, later outside. They continue in the fishery until the following spring and summer, when they spawn and disappear at the age of 1 year. During this time they grow to a length of about 120 mm; remain at this size through the winter, resume growth in the spring; and, after a rapid differentiation of the size of the sexes, spawn at length about 130 to 170 mm for the males and 135 to 190 mm for the females. Their fate is unknown, but that they disappear from the commercial catch following spawning is undoubted.

During the breeding season in the inside waters of Georgia there is a much greater proportion of females than males, while in the outside waters there is a greater proportion of males.

In Georgia at the beginning of the breeding season there is evident a differential behavior of the males and females; a differential growth rate between the sexes, with the females outstripping the males; and a change in the length frequency groupings from a wide to a very narrow range.

The common shrimp is most abundant in the coastal waters near river mouths or delta regions. It is omnivorous in its feeding habits. At present the shrimp fishery does not appear to show serious depletion, consequently increased stringency of existing laws is not imperative.

In the life history of the shrimp there are two factors favoring depletion—the short life span and exposure to fishing at all times. On the other hand, there are two factors opposing depletion—the extended breeding season and the large number of eggs produced. The most recent and at present one of the most decisive factors of the environment is the fishing of man. To date the favoring factors have maintained a vast shrimp population. With a more and more intensive fishery, the unfavorable factors must at some time become the more powerful. Because of the short life of the common shrimp, depletion, when it appears, will probably run a disastrously rapid course; consequently vigilance in safeguarding the industry is necessary. Against this time, methods of protection must be carefully planned.

There are four types of regulation applicable to the shrimp fishery; namely, closed seasons, closed areas, size limits, and restriction of gear. The fishery records of the various States are entirely inadequate to permit an analysis of abundance. For the safety of the shrimp industries it is imperative that this lack of catch records should speedily be remedied. It is recommended that all States collect on a standard form uniform records of the daily catch of each fisherman; certain of the States are now working on this problem. It is only by such records that any accurate indication of threatened depletion may be detected.

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